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Series on Harmonization of Regulatory Oversight in Biotechnology, No.22

CONSENSUS DOCUMENT ON THE BIOLOGY OF PINUS STROBUS L. (EASTERN WHITE PINE)

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Also published in the Series on Harmonization of Regulatory Oversight in Biotechnology:

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OECD Environment, Health and Safety Publications

Series on Harmonization of Regulatory Oversight in Biotechnology

No. 22

Consensus Document on the Biology of *Pinus Strobus L.* (Eastern White Pine)

Environment Directorate

Organisation for Economic Co-operation and Development

Paris 2002

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FOREWORD

The OECD's Working¹ Group on Harmonization of Regulatory Oversight in Biotechnology decided at its first session, in June 1995, to focus its work on the development of *consensus documents* which are mutually acceptable among Member countries. These consensus documents contain information for use during the regulatory assessment of a particular product. In the area of plant biosafety, consensus documents are being published on the biology of certain plant species, on selected traits that may be introduced into plant species, and on biosafety issues arising from certain general types of modifications made to plants.

This document addresses the biology of *Pinus strobus* L. (Eastern White Pine). It contains general information as well as more specific information on taxonomy, reproductive biology, crosses, genetics, ecology and domestication. It is intended for use by regulatory authorities and others who have responsibility for assessments of transgenic plants proposed for commercialisation, and by those who are actively involved with genetic improvement and intensive management of the genus.

Canada served as lead country in the preparation of this document. It has been revised on a number of occasions based on the input from other member countries. The Joint Meeting of the Chemicals Committee and the Working Party on Chemicals, Pesticides and Biotechnology subsequently recommended that this document be made available to the public.

¹ In August 1998, following a decision by OECD Council to rationalise the names of Committees and Working Groups across the OECD, the name of the "Expert Group on Harmonization of Regulatory Oversight in Biotechnology" became the "Working Group on Harmonization of Regulatory Oversight in Biotechnology."

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Preamble

OECD member countries are now commercialising and marketing agricultural and industrial products of modern biotechnology. They have identified the need for harmonization of regulatory approaches for the assessment of these products, in order to avoid unnecessary trade barriers.

In 1993, **Commercialisation of Agricultural Products Derived through Modern Biotechnology** was instituted as a joint project of the OECD's Environment Policy Committee and its Committee on Agriculture. The objective of this project is to assist countries in their regulatory oversight of agricultural products derived through modern biotechnology – specifically in their efforts to ensure safety, to make oversight policies more transparent and efficient, and to facilitate trade. The project is focused on the review of national policies, with respect to regulatory oversight, that will affect the movement of these products into the marketplace.

The first step of this project was to carry out a survey concentrating on national policies in regard to regulatory oversight of these products. Data requirements for products produced through modern biotechnology, and mechanisms for data assessment, were also surveyed. The results were published in *Commercialisation of Agricultural Products Derived through Modern Biotechnology: Survey Results* (OECD, 1995).

Subsequently, an OECD workshop was held in June 1994 in Washington, D.C. with the aim of improving awareness and understanding of the various systems of regulatory oversight developed for agricultural products of biotechnology; identifying similarities and differences in various approaches; and identifying the most appropriate role for the OECD in further work towards harmonization of these approaches. Approximately 80 experts in the areas of environmental biosafety, novel food safety and varietal seed certification, representing 16 OECD countries, eight non-member countries, the European Commission and several international organisations, participated in the workshop. *Report of the OECD Workshop on the Commercialisation of Agricultural Products Derived through Modern Biotechnology* was also published by the OECD in 1995.

As a next step towards harmonization, the Working Group on Harmonization of Regulatory Oversight in Biotechnology instituted the development of **consensus documents** that are **mutually recognised** among member countries. The purpose of these documents is to describe common elements in the safety assessment of a new plant variety developed through modern biotechnology, to encourage information sharing and prevent duplication of effort among countries. These common elements fall into three general categories: the biology of the host plant species, or crop; the introduced genes and gene products conferring the novel trait; and biosafety issues arising from the introduction of certain general trait types into plants.

This consensus document is a “snapshot” of current information that may be relevant in a regulatory risk assessment. It is meant to be useful not only to regulatory officials, as a general guide and reference source, but also to industry and others carrying out research and product development.

It is anticipated that this consensus document and others in the plant biology series, together with the relevant consensus documents on genes and products that confer novel traits in plants as well as those providing information on biosafety issues arising from the use of general trait types in plants, will be of use in the biosafety assessment of genetically modified plants.

Reference to two other OECD publications that have been published in recent years will also prove useful. *Traditional Crop Breeding Practices: An Historical Review to Serve as a Baseline for Assessing the Role of Modern Biotechnology* presents information concerning 17 different crop plants. It includes sections on phytosanitary considerations in the movement of germplasm and on current end uses of the crop plants. There is also a detailed section on current breeding practices. *Safety Considerations for Biotechnology: Scale-Up of Crop Plants* provides a background on plant breeding, discusses scale dependency effects, and identifies various safety issues related to the release of plants with “novel traits”.²

To ensure that scientific and technical developments are taken into account, OECD countries have agreed that consensus documents will be updated regularly. Additional areas relevant to the subject of each consensus document will be considered at the time of updating.

Users are therefore invited to provide relevant new scientific and technical information, and to make proposals concerning additional areas that might be considered in the future. ***A short, pre-addressed questionnaire is included at the end of this document. The information requested should be sent to the OECD at one of the addresses shown.***

2. For more information on these and other OECD publications, contact the OECD Publications Service, 2 rue André-Pascal, 75775 Paris Cedex 16, France. Fax: (33) 01.49.10.42.76; E-mail: PUBSINQ@oecd.org; or consult <http://www.oecd.org>

Section I – General Information

This consensus document addresses the biology of eastern white pine (*Pinus strobus* L.), referred to hereafter simply as eastern white pine (*pin blanc* in French Canada). Eastern white pine is one of the most valuable tree species in eastern North America where its easily machined, uniform-textured wood is unsurpassed for doors, windows, panelling, mouldings and cabinet work (Mullins and McKnight, 1981; Farrar, 1995). The species played a major role in the settlement and economic development of New England and the Atlantic Provinces as England reserved all large eastern white pine suitable for masts under the "Broad Arrow" policy, starting in the late 1600's (Johnson, 1986). Eastern white pine also responds well to nursery culture and is commonly used for reforestation, urban forestry and Christmas tree plantations.

The general biology of eastern white pine is described in the context of the species' role in natural forests and its domestication in planted stands. Taxonomic and evolutionary relationships with other *Pinus* species are described. Reproductive biology is described with a focus on aspects of mating system, gene flow, seed production and natural stand establishment. The current knowledge of genetic variation within the species is reviewed, highlighting the importance of geographic variation patterns and the potential for improvement by means of recurrent selection breeding strategies. The tremendous biological diversity and the complexity of ecological interactions with higher and lower flora and fauna are discussed. While eastern white pine has been commonly planted within its natural range, the extent of reforestation has been limited by susceptibility to white pine weevil (*Pissodes strobi*) and blister rust (*Cronartium ribicola*). Domestication and operational breeding activities are also reviewed. Crossing with other related white pine species offers some promise of producing hybrids with increased resistance to both the weevil and blister rust. While white pine reforestation is currently based on seed propagation, vegetative propagation techniques are available and research continues into regeneration from somatic embryos.

Canada was the lead country in preparation of this document. It is intended for use by regulatory authorities and others who have responsibility for making assessments of transgenic plants proposed for commercialisation, and by those who are actively involved with genetic improvement and intensive management of this species.

Section II – Taxonomy and Natural Distribution

A. Taxonomy and nomenclature

The genus *Pinus* L. (family Pinaceae) is widely distributed throughout the Northern Hemisphere, from the arctic circle south to Guatemala, the West Indies, North Africa and Indonesia, with as many as 100 species being recognised (Krüssmann, 1985). The genus was first classified on evolutionary characteristics by Shaw (1914), and taxonomists have since followed his general separation of the genus into two groups: *Haploxylon* Koehne, and *Diploxylon* Koehne; commonly called the "soft" (or "white") and "hard" pines, respectively, based on the presence of one or two vascular bundles in the leaves. Shaw's original subdivision of these groups has been reworked by different authorities (e.g., Pilger, 1926; Duffield, 1952; de Ferré, 1965; Landry, 1974b, 1978), but botanists in recent years have generally recognised the classification described by Little and Critchfield (1969, 1986), who place eastern white pine, *Pinus strobus* L., within the subgenus *Strobus* Lemm. (equivalent to subgenus *Haploxylon*), section *Strobus*, subsection *Strobi* Loud. Also known as northern pine and, in parts of Europe, as Weymouth pine, after Lord Weymouth, the species nomenclature has remained virtually undisputed since the publication of the *Species Plantarum* (Linné, 1753), although Provancher later referred to it as *Pinus alba Canadensis* Prov. (Landry, 1974a).

Several horticultural forms have been named, although none are currently recognised with varietal status (Krüssmann, 1985). Only one variety has been commonly described, *Pinus strobus* L. var. *chiapensis* Martinez, the Chiapas white pine, occurring in the mountains of southern Mexico and Guatemala. While similar morphologically, it is physiologically quite different (Wright, 1970) and now generally recognised as a separate species, *Pinus chiapensis* (Martinez) Andresen (Griffiths, 1994; Perry, 1991).

B. Natural distribution

Eastern white pine has the largest range of any North American member of subgenus *Strobus*, and is the only species in the subgenus occurring on the eastern side of the continent. It extends from Newfoundland and Quebec, west to central Ontario and south-eastern Manitoba, south to Minnesota, north-eastern Iowa, northern Illinois, north-western Indiana, Ohio, Pennsylvania, and New Jersey, and south in the Appalachian Mountains to western North Carolina, northern Georgia, and Tennessee. Overall, the species spans a north-south range of over 1900 km, and about the same distance inland from the Atlantic coast (Critchfield and Little, 1966; Mirov, 1967; Wendel and Smith, 1990). The natural range of eastern white pine is illustrated in the map given in Figure 1.

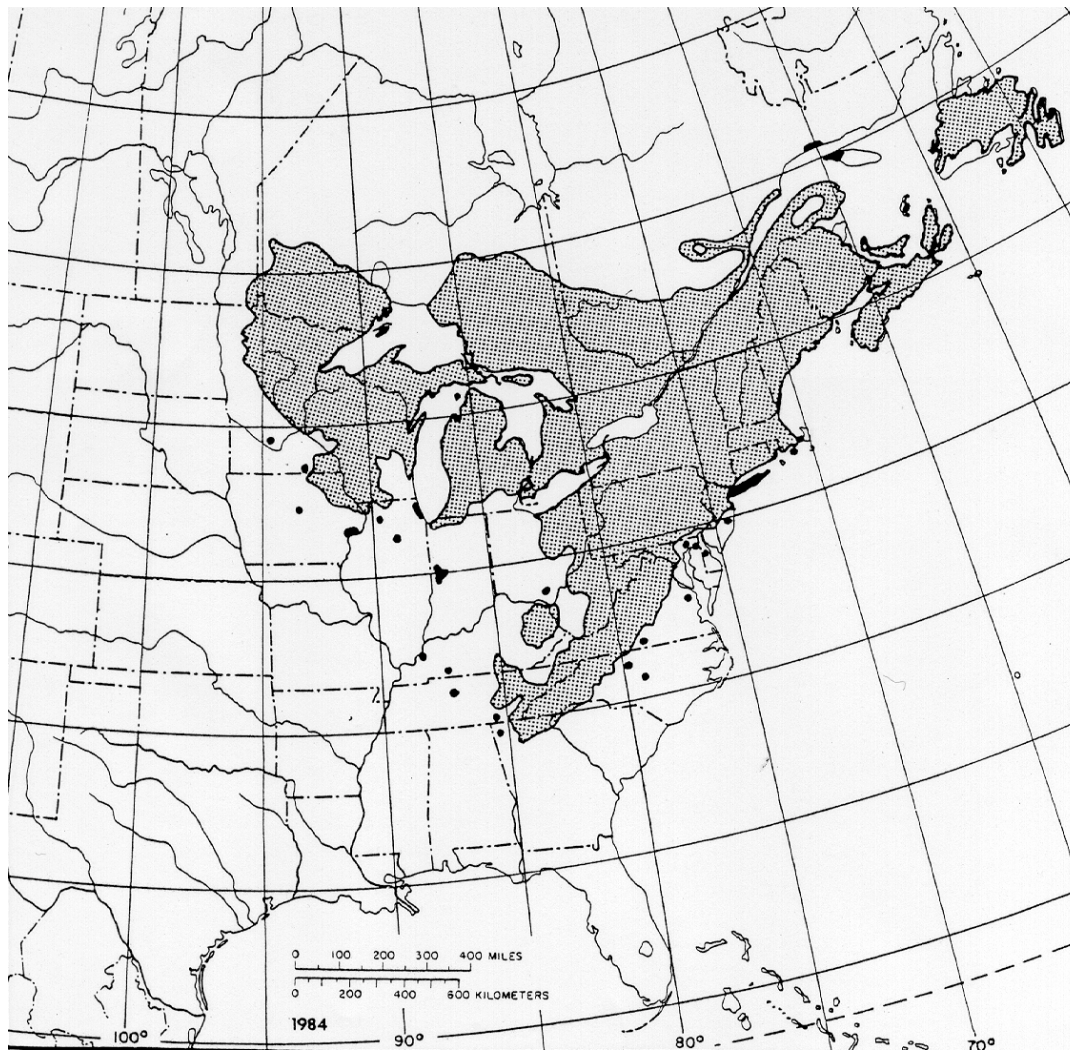


Figure 1. The natural range of eastern white pine (from Wendel and Smith, 1990)

C. Evolution and migrational history

Conifers probably originated around the periphery of the north Pacific basin (Li, 1953). Fossil records indicate that divergence of modern genera in Pinaceae occurred some 135 million years ago during the late Jurassic or early Cretaceous period (Florin, 1963), and *Pinus* is believed to be the oldest genus in the family (Miller, C.N. 1976, 1988). Opinion on whether the first pines were of subgenus *Strobus* or *Pinus* remains mixed, and the centre of origin of pines is uncertain. Millar and Kinloch (1991) describe the rapid spread of pines over dry, temperate paleolatitudes during the Cretaceous period, prior to the separation of North America from Europe, during which all sections and subsections appear to have originated. In the early Tertiary period, global climate changes favoured the spread of angiosperms, which adapted to the hot, humid conditions. These climate changes fragmented and displaced the pines into drier refugia at upper and lower latitudes, and scattered refugia at mid-latitudes, creating secondary centres of origin. Ancestors of *P. strobus* and *P. monticola* were isolated in northern refugia from other species in section *Strobi* that were isolated in the south. The warm, tropical conditions changed rapidly at the end of the Eocene epoch and pines became re-established at middle latitudes. These abrupt changes in climate had drastic impacts on the gene structure of genetic variation of forest populations, with isolated populations continuing their short-term evolution (Critchfield, 1984).

Section III – Reproductive Biology

A. Reproductive development

Eastern white pine is monoecious. Production of female strobili occurs as early as 4 years (Buckingham, 1963) while pollen production may not start for 10 to 20 years (Wright, 1970). As in other pines, development of the reproductive structures follows a 3-year cycle. Pollination occurs in the spring of the second year, with fertilisation delayed until the following spring, and seeds maturing in the fall of the third year (Owens and Blake, 1985). No other conifer genus has had its reproductive cycle described more often or more thoroughly, and eastern white pine was among the first pines to be studied in detail (Ferguson, 1901, 1904). Reproductive buds begin as axillary bud primordia within a complex long-shoot bud, consisting of a series of cataphylls initiated throughout the growing season. Many of the cataphylls support an axillary apex that first initiates a series of bud scales, then differentiates into a short (fascicular) shoot, seed or pollen cone, or lateral long shoot bud. Those axillary buds initiated at the base of the long shoot bud in the spring or early summer will differentiate into short-shoot or pollen-cone buds. Subsequent axillary buds differentiate only into short shoots. The distal axillary buds remain undetermined through winter dormancy of the long shoot bud, differentiating immediately the following spring into lateral long shoot or seed cone buds (Owston, 1969; Owens and Molder, 1977). While seed-cones generally develop on vigorous shoots in the upper portion of the crown, distribution of reproductive structures is often extremely variable.

Pollen development and meiosis does not occur until the spring of the second year as pollen cones resume their development. The ripening strobili turn light brown before releasing their pollen over a 1-week period. The seed cones also resume development in the spring, and are visible at the distal end of elongating long shoots. The developmental morphology of reproductive structures was well documented with colour photographs by Ho (1991). Wind-borne pollen grains landing on the receptive seed cone pass between the bracts and sift down to the surface of the micropylar arms, entering the micropyle by means of a pollen drop. The pollen germinates, but becomes dormant before the male gametes form (Owens and Molder, 1977). Fertilisation occurs about 13 months after pollination. Simple polyembryony in eastern white pine results from the fertilisation of 2 to 3 archegonia in each megagametophyte. The seed cones mature and seeds are dispersed in August or September of the same year (Krugman and Jenkinson, 1974).

B. Mating system and gene flow

Eastern white pine is a wind-pollinated, monoecious species, and outcrossing is by far the most prevalent mating system, although there are relatively few detailed studies. Isozyme studies of populations in Québec indicated a high rate of outcrossing, with most loci in Hardy-Weinberg equilibrium (Beaulieu and Simon, 1994, 1995).

Gene flow in *Pinus* is mediated by very small pollen grains, 40-60 μm at their widest point (Eisenhut, 1961), whose two air sacs and low density make them well-adapted for aerial transport (Di-Giovanni and Kevan, 1991). Various studies of pollen dispersal in conifers indicate that over 90% of the pollen comes to rest less than 100 m from the source (Wright, 1976). Nevertheless, conifer pollen may remain viable for several days and a substantial quantity may travel great distances (Lindgren et al., 1995; Lindgren and Lindgren, 1996). Gregory (1973) cites reports that pollen of *Pinus* and *Picea* may travel as

far as 600 to 1 000 km, and several authors have concluded that isolation distances of less than 1 km often have little impact on contamination rates in conifer seed orchards (see review by Di-Giovanni and Kevan, 1991).

C. Seed production

Eastern white pine normally begins seed production at 5 to 10 years of age (Fowells, 1965; Sargent, 1965), although little pollen is produced during the early years of flowering (Wendel and Smith, 1990). The interval between heavy seed crops is usually 3 to 10 years (Krugman and Jenkinson, 1974; Wendel and Smith, 1990), becoming less frequent as trees become over mature (Horton and Bedell, 1960). A study in Germany recorded seed production as high as 73 kg/ha in a 90-year-old stand (Messer, 1956), while in Maine, a stand considered to be intermediate in density with a basal area of 28 m²/ha produced over 4.4 million seeds per hectare in a "bumper" year (Graber, 1970). This corresponds to 69kg/ha seed.

Initiation of seed dispersal is weather and site dependent, and may be delayed by cool, moist weather. Most of the seeds are dispersed in the fall during a 4 to 8 week period (Horton and Bedell, 1960; Graber, 1970). The seeds are mature when cone moisture content decreases below 200% on a dry-weight basis, but cone specific gravity is not a reliable indicator of maturity (Barnett, 1988). A short "artificial ripening" period can increase yield and quality of seed from immature cones (Bonner, 1986, 1991; Barnett, 1988).

The seeds are winged and dispersal distances depend greatly on local and prevailing wind patterns (Rudis et al., 1978). The seeds may travel more than 60 m within a closed stand, and over 200 m in the open (Wilson and McQuilkin, 1963), although most of the seed will fall within a distance equivalent to the height of the seed tree (Horton and Bedell, 1960). The seeds themselves are smaller than those of most other "soft" pines, but similar to those of *P. monticola*, with average cleaned seed weight of about 17 g/1000 seeds (Krugman and Jenkinson, 1974).

D. Natural regeneration

Eastern white pine seeds exhibit varying degrees of embryo dormancy that may be broken by exposure to low temperatures under moist conditions, i.e., cold stratification (Krugman and Jenkinson, 1974; Nelson et al., 1980; Mittal et al., 1987; Downie and Bergsten, 1991). The recommended treatment for nursery sowing is stratification for 60 days at 1 to 5° C (Krugman and Jenkinson, 1974). Under natural conditions, over-winter stratification on the forest floor breaks seed dormancy and germination of most seeds occurs in late spring of the following year (Stiell, 1985).

Germination is epigeal. Moist mineral soil, polytrichum moss, and shortgrass cover of light to medium density are favourable seedbeds. Establishment on less favourable seedbeds, such as pine litter and lichen, will occur under partial shade and/or surface. Shelterwood harvesting systems provide good protection during initial establishment with sufficient light for subsequent growth of young stands (Wilson and McQuilkin, 1963; Corbett, 1994). Optimum conditions are provided when moist mineral seedbeds have greater than 20% of full sun, but where partial shade reduces surface temperatures and provides better moisture conditions (Lancaster and Leak, 1978). Low seedling densities are associated with competition from broad-leaved shrubs, herbaceous vegetation, tolerant conifer species and feather mosses (Carleton et al., 1996). White pine regeneration is usually associated with its proportion in the overstorey (Kittredge and Ashton, 1990), and under old-growth conditions is likely to become at least partially uneven-aged and self replacing, facilitated by local disturbances and continuous recruitment (Quinby,

1991; Ziegler, 1995). Older trees have increased their ability to recover from long periods of suppression (Abrams and Orwig, 1996).

E. Vegetative reproduction in nature

Eastern white pine does not regenerate vegetatively under natural conditions (Wendel and Smith, 1990).

Section IV – Crosses

Other members of subgenus *Strobus* do not occur within the natural range of eastern white pine, and introgressive hybridisation does not occur. Most artificial crosses among North American members of subsection *Strobi* have been successful, the exception being those involving *Pinus lambertiana* Dougl. (Critchfield, 1986; Critchfield and Kinloch, 1986). Successful crosses involving eastern white pine are summarised in Table 1. Only two of these hybrids have been widely field tested, including that with *P. monticola* Dougl. and its reciprocal, and with *P. wallichiana* A.B. Jackson (formerly *P. griffithii* McClell.) and its reciprocal (Kriebel, 1983). No successful hybrid crosses have been reported with species in other sections of *Pinus* (Critchfield, 1975).

Table 1. Summary of successful crosses with *P. strobus*

Species	Origin	References
<i>P. monticola</i> Dougl. ex D.Don.	western US and Canada	Wright, 1959, 1970; Kriebel, 1972b
<i>P. wallichiana</i> A.B. Jackson (syn <i>P. griffithii</i> McClell., <i>P. excelsa</i> Wallich ex D.Don), hybrid = <i>P. × schwerinii</i> Fitschen	Himalayas	Wright, 1959, 1970; Kriebel, 1972b; Garrett, 1979; Zsuffa, 1979b; Blada, 1992
<i>P. ayacahuite</i> Ehrenb.	Mexico, Guatemala	Johnson and Heimburger, 1946; Wright, 1959; Garrett, 1979
<i>P. parviflora</i> Sieb. and Zucc. hybrid = <i>P. × hunnewelli</i> A.G. Johnson	Japan	Johnson, 1952; Wright, 1959
<i>P. peuce</i> Griseb.	S.E. Europe	Fowler and Heimburger, 1958; Radu, 1976; Santamour and Zinkel, 1978
<i>P. flexilis</i> James (only one parent successful, may in fact be <i>P.</i> <i>strobiformis</i> Engelm.)	western US and Canada	Wright, 1959; Kriebel, 1972a

When hybrids are made successfully, they sometimes display hybrid vigour and out-perform the parent species (Wright, 1970; Kriebel, 1983). However, more important than increased vigour, hybrids with *P. wallichiana*, *P. peuce*, and *P. parviflora* have demonstrated potential resistance to blister rust (Heimburger, 1962, 1972; Patton, 1966; Zsuffa, 1979a), and those with *P. peuce* and *P. monticola* may be less susceptible to weevil attack (Heimburger and Sullivan, 1972a, b). While hybridity barriers within the hard pines are generally associated with pollen tube incompatibility, crossability barriers among the white pines are more often the result of embryo inviability (Kriebel, 1972a; Shafer and Kriebel, 1974).

Section V – Genetics

A. Cytology

Vegetative cells are normally diploid, with $2n = 24$ chromosomes (Saylor, 1983). Saylor and Smith (1966) reported that 4% of cells displayed meiotic irregularities such as precocious disjunction, lagging chromosomes, and inversion bridges.

B. Genetic variation

B.1 Population-level variability

While seed source testing of eastern white pine began in the United States in 1937 (Pauley et al., 1955), provenance tests with range-wide sampling did not begin until the mid-1950's. Around this time, the USDA Forest Service initiated a large provenance test, in which 30 seed collections representing all parts of the natural range were established by co-operators in 13 test plantations in the United States and 2 in Ontario (Sluder, 1963; Wright et al., 1963; Funk, 1965; Fowler and Heimburger, 1969b; King and Nienstaedt, 1969; Genys, 1977). Shortly after, another provenance test involving more seedlots on fewer test sites was started by the University of Maryland (Genys, 1968; Genys et al., 1978). Encouraging early results from these tests, indicating the superiority of sources from the South Appalachians, led to intensive testing of these sources under the leadership of Michigan State University (Roth and Carson, 1976; Wendel and Cech, 1976; Wright et al., 1976; Gall and Thor, 1977).

While correlations with latitude have sometimes been noted on a range-wide basis (Genys, 1987, 1991), relative differences in height and diameter between northern and southern sources diminish somewhat with age (Demeritt and Kettlewood, 1976; Demeritt and Garrett, 1996). Clinal patterns are often less distinct over shorter distances with the presence of non-clinal adapted ecotypes (Genys, 1968; Garrett et al., 1973; Thor, 1975; des Bordes and Thor, 1979; Funk, 1979). In Nebraska, seed sources from the southern Appalachians demonstrated correlations with latitude for needle length and reproductive phenology, a weak geographic pattern for variation in height, and none for survival (Sprackling and Read, 1976; Van Haverbeke, 1988). Ryu and Eckert (1983) investigated the genetic structure of 27 of these provenances for eight foliar enzymes coded by 12 loci and found four clusters of provenances, three of which may be representative of populations adapted to differing geographic and climatic conditions. The results of this study support the indication of ecotypic variation among three provenances in the southern Appalachians for growth performance and physiological variables, and suggest that these areas may have been isolated refugia during glaciation. Elsewhere in the northern part of the range, sources from the Atlantic coast outperformed those from further inland, while some exceptional sources originated from as far south as Georgia and Tennessee (Zsuffa, 1975; Abubaker and Zsuffa, 1991).

Southern provenances have heavier seeds (Genys, 1968), require longer periods of stratification before germinating (Fowler and Dwight, 1964; Graber, 1965) and longer chilling periods to break bud dormancy (Mergen, 1963), set bud later (Santamour, 1960) and are less cold hardy (Maronek and Flint, 1974). Wood specific gravity was negatively correlated with height and diameter, but differences among sources were small (Lee, 1974; Gilmore and Jokela, 1978; Olson et al., 1981). No variation could be detected for foliar monoterpene content, and no geographic pattern was evident for variation in cortical monoterpenes (Gilmore and Jokela, 1979).

Provenance tests have shown some variation in susceptibility to white pine weevil, but give little indication that resistant populations can be identified (Garrett, 1972, 1973; Connola and Beinkafner, 1976; Wilkinson, 1983b). Selective thinning of susceptible parents (dominant "wolf" trees) from a stand can increase the level of resistance in the progeny generation, and taller families tend to be more weevil resistant (Ledig and Smith, 1981). Although there is ample evidence of genetic control of susceptibility to weevil, the actual mechanism(s) of resistance remains uncertain.

B.2 Individual-level variability

While variation among provenances is important in determining the risks and benefits of transferring seed sources, genetic improvement from mass selection relies primarily on variation within-populations as the source of genetic gains. The partitioning of genetic variance among and within populations is greatly influenced by the range of adaptive variation sampled by the tested provenances and the age at which the test material is assessed. Range-wide and regional studies have typically demonstrated strong heritabilities, sufficient to predict moderate to high genetic gains, although heritability tends to be lower for older material (Thor, 1975; Adams and Jolly, 1978; des Bordes and Thor, 1979; Olson et al., 1981). Hierarchical sampling of populations over a more limited range in Québec and Ontario showed that population differences were greatest for allozyme markers, where 98% of the variation was within populations (Beaulieu et al., 1996). Growth traits, on the other hand, demonstrated variation within stands to be about half as great as that among populations (Li, P. et al., 1997). Individual heritability for height declined from 0.547 at age 4 in the nursery, to 0.187 at age 10 in the field (Beaulieu et al., 1996). In an incomplete diallele cross experiment among individuals of a local provenance, Kriebel et al. (1972) found that narrow-sense heritability for height growth declined from 0.59 at age 1 to 0.16 at age 3, and that while dominance effects were small, maternal effects were rather large. By age 13, it was still possible to achieve substantial gains by family selection (Kriebel, 1978).

Significant genotype-environment interactions have been reported in eastern white pine, but the magnitude of the interaction variance is generally low (less than 2%). Genetic correlations between sites tend to be high, indicating that family ranks are stable across sites (des Bordes and Thor, 1979; Beaulieu et al., 1996; Demeritt and Garrett, 1996).

The search for weevil-resistance has always been a driving force behind genetic testing in eastern white pine (Pauley et al., 1955; Wright and Gabriel, 1959). Early studies indicated that selection for weevil resistance might be done indirectly by assessment of bark thickness (Kriebel, 1954; Gerhold, 1962, 1966) and/or leader morphology (Stroh, 1964, 1965), but when these are corrected for tree size, they appear to be of little value for effective selection (Wilkinson, 1983a, 1984). Other studies have identified that concentrations of various cortical oleoresin compounds are correlated with weevil susceptibility, but even these criteria leave much of the variation in weevil susceptibility unexplained (van Buijtenen and Santamour, 1972; Santamour and Zinkel, 1976, 1978; Bridgen et al., 1979; Wilkinson, 1979, 1980, 1984, 1985).

C. Inbreeding depression and genetic load

Eastern white pine is an outcrossing species that carries a fairly heavy load of deleterious recessive genes. Individuals are generally self-compatible, so that this genetic load is revealed by self-fertilisation (Fowler, 1965a; Fowler and Heimburger, 1969a). Although there is no reduction in numbers of filled seeds after selfing (Fowler, 1965b), selfed seedlings may be stunted, slow growing, chlorophyll-deficient and deformed (Johnson, 1945; Patton and Riker, 1958a; Fowler, 1965b). Simple polyembryony in eastern white pine results from 2 to 3 archegonia in each megagametophyte. As only one embryo normally germinates from the mature seed, it is likely that competition during seed development eliminates many weaker embryos, including those resulting from self-fertilisation (Willson and Burley, 1983). An isozyme study of populations in Quebec demonstrated a high outcrossing rate, with few loci deviating from Hardy-Weinberg equilibrium (Beaulieu and Simon, 1995). This study found evidence of family structure, with greater inbreeding in the filial than in the parental population, although few of the inbred genotypes were expected to reach reproductive age, due to natural selection.

D. Breeding programs

Eastern white pine has been a candidate for tree breeding efforts throughout its native range. In the northern part of its range, throughout eastern Canada, the north-eastern US and the Lake States, planting programs have been limited by susceptibility to weevil and rust, so that seed orchards exist throughout this region (Zsuffa, 1985, 1986; Garrett, 1986; Miller, 1987; Eckert and Kuser, 1988; Lamontagne, 1992; Nielsen et al., 1995; Smith et al., 1997; *pers. comm.* R. Stine, Minnesota Tree Improvement Cooperative) and, the level of effort reflects the restricted size of planting programmes. Pests are less of a problem for breeding programs in the Central States, where selection and hybrid breeding can focus on vigour (Kriebel, 1983). Outside of the natural range in Europe, selection within southern Appalachian provenances and crossing with other white pines, such as *Pinus wallichiana*, are used to develop fast-growing, rust-resistant hybrids (Kriebel, 1983).

Most seed orchards currently in production were established by grafting cuttings from plus-trees, and their establishment in cultivated field environments. Grafting success is usually very high. Flowering in field orchards can be enhanced by means of cultural treatments such as fertilisation (Hocker, 1962; Stephens, 1964). Flowering of young white pine grafts can also be stimulated by means of various cultural treatments, particularly those involving gibberellin $A_{4,7}$, and this has facilitated the turnover of breeding cycles (Ho and Schnekenburger, 1992; Ho and Eng, 1995).

E. Conservation of genetic resources

Domestication of a key species such as eastern white pine can influence diversity of genetic resources (1) indirectly, by the method of seed collection, extraction, and storage, and by nursery and plantation culture; and (2) directly, by intentional selection to increase the frequency of genes for desirable traits (Morgenstern, 1996). The inadvertent loss of genes by natural processes and human activity can have negative consequences on the adaptability of populations and the potential for future gains from breeding.

A long history of exploitation has resulted in white pine forest fragmentation and reduction of population sizes, particularly at the northern limits of the species range (Buchert, 1994; Buchert et al., 1997). Throughout most of the range of white pine, *in situ* conservation of genetic resources is practised by protection of ecological reserves, special areas, and parks (Pollard, 1995), and integrated with

domestication activities that control the movement of seed, active management of existing stands to maintain biological diversity, and protection of isolated, small populations (Mosseler, 1995; Nieman et al., 1995).

Ex situ conservation, by cryopreservation of germplasm, by off-site maintenance of populations in arboreta, seed orchards and clone banks, and by multi-population breeding strategies (Eriksson et al., 1993; Namkoong, 1995), has been practised to a much lesser extent, although many provenances and families of eastern white pine are now represented in field tests and seed bank collections (Plourde et al., 1995). Such "active" forms of gene management must be accelerated in preparation for response to rapid environmental and climate changes (Ledig and Kitzmiller, 1992).

Section VI – Ecology and associated species

Much of the information in this section originates from the excellent monograph on silvics of the species by Wilson and McQuilkin (1963). Other citations are given when appropriate when specific information is attributable to other sources.

A. Habitat

A.1 Climate

Eastern white pine's natural range is cool and humid. July average temperatures are between 18 to 25° C, and annual precipitation varies from about 510 mm in northern Minnesota to 2030 mm in northwestern Georgia, with at least half occurring between April and November. Average snowfall varies from less than 15 cm in the southern portion of the range to over 250 cm in the northeast (Wendel and Smith, 1990). There is a surplus of moisture in all seasons.

A.2 Soils and site type

Eastern white pine grows on a wide variety of soils throughout its range, from dry sands and rocky ridges, to sphagnum bogs, although it grows best on moist sandy or loamy soils. Soils within the range are derived from granites, gneisses, schists, sandstones, and, to a lesser extent, phyllites, slates, shales and limestones. Eastern white pine competes best on medium-textured, well-drained soils of moderate site quality, with surface pH between 4.0 and 7.5, and which are not sufficiently rich to support strong hardwood competition, or where competition is reduced during the establishment period, such as on old fields, burnt or blow-down areas (Horton and Bedell, 1960; Mader, 1986).

In the northeast portion of the range, eastern white pine generally occurs below 450 m above sea level, whereas in Pennsylvania, elevations vary between 150 and 600 m. In the southern Appalachians, stands generally occurs between 370 and 1070 m. Except in Pennsylvania and the southern Appalachians where stands are found on northerly aspects or in the shelter of stream bottoms. White pine sites are not generally restricted by slope or aspect.

B. Synecology and associated species

Eastern white pine may form pure stands or occur as a major stand component of several stand types in association with other conifers and hardwoods such as: red pine (*Pinus resinosa*), balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), white spruce (*P. glauca*), red oak (*Quercus rubra*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), hemlock (*Tsuga canadensis*), and chestnut oak (*Quercus prinus*). Eastern white pine may also be found as a lesser stand component with jack pine (*Pinus banksiana*), pitch pine (*P. rigida*), shortleaf pine (*P. echinata*), sweet birch (*Betula lenta*),

trembling aspen (*Populus tremuloides*), large-tooth aspen (*P. grandidentata*), black cherry (*Prunus serotina*), black oak (*Quercus velutina*), white oak (*Quercus alba*), and various hickories (*Carya* spp.) (Horton and Bedell, 1960; Eyre, 1980). The occurrence of associations depends on both site conditions and history of disturbance (Stiell, 1985).

Pure stands of eastern white pine usually support sparse cover of understory vegetation, but many species may be found under mixed stands, particularly those associated with hardwood associates. On drier sites, ground vegetation may consist of one or more species of blueberries (*Vaccinium* spp.), teaberry (*Gaultheria procumbens*), dwarf bush-honeysuckle (*Diervilla lonicera*), sweetfern (*Comptonia peregrina*) bracken fern (*Pteridium aquilinum*), clubmoss (*Lycopodium* spp.), and broom sedge (*Andropogon virginicus*). Richer, moist sites will often support ground cover of woodsorrels (*Oxalis* spp.), partridgeberry (*Mitchella repens*), wild sarsaparilla (*Aralia nudicaulis*), jack-in-the-pulpit (*Arisaema* spp.), and hay-scented fern (*Dennstaedtia punctilobula*). Intermediate sites may have varying amounts of the above species, together with dogwoods (*Cornus* spp.) and false lily-of-the-valley (*Maianthemum canadense*).

C. Competition and stand structure

Eastern white pine is distributed over a larger area than any other North American white pine, and has demonstrated its capacity to grow and compete under a wide variety of environmental conditions (Stiell, 1978, 1985). While it is a long-lived successional species and may be a component of climax forest types, it is also well-known as a pioneering species on old fields in New England. Eastern white pine is considered intermediate in its tolerance to shade, somewhat less tolerant than eastern spruces and more tolerant than its pine associates (Daniel et al., 1979). Vegetative competition for light and soil moisture is critical during seedling establishment, and remains important well into the life of the stand. Sites that have a high capability for productivity for pine tend to have greater competition. Competition problems are most severe on heavier, moist, rich soils, where eastern white pine will perform well, only if natural disturbance, such as fire, or silvicultural site treatments allow the pine to become established well ahead of the hardwoods that normally occupy such sites (Horton and Bedell, 1960; Little et al., 1973; Stiell, 1985; Chapeskie et al., 1989).

D. Ecosystem dynamics

Several abiotic factors also interact with eastern white pine in forest ecosystems. While older trees have thick, heat-resistant bark, the thinner bark on exposed roots and younger stems is sensitive to fire. Even light fires can have a detrimental impact on seed supply, but may also reduce hardwood competition and leave a seedbed that is more conducive to the establishment of new germinants. Frost heaving can cause severe damage, particularly to container seedlings planted on finer-textured soils. Eastern white pine is relatively wind firm, but may suffer storm breakage if the stand has been recently thinned. While it is widely held that eastern white pine is sensitive to ozone and sulphur dioxide pollution (Gerhold, 1977), recent data in the literature are somewhat contradictory and suggest that injury and growth losses may be strongly genotype and site dependant (Houston and Stairs, 1973; Genys and Heggstad, 1978, 1983; Townsend and Dochinger, 1982; Usher and Williams, 1982; Yang et al., 1982, 1983; Eberhardt et al., 1988; Rezabek et al., 1989; Bartholomay et al., 1997; Hogsett et al., 1997).

The following table (2) shows species interactions with eastern White Pine.

Table 2. Interactions

Insects	
Common name	Agent
White pine weevil [Sullivan, 1961; Sun and Nigam, 1972; Sunandram et al., 1972; Berry and Steill, 1976; Sunandram, 1977; Stiell, 1979; Martineau, 1984; deGroot, 1985; Drooz, 1985; Gross, 1985a; Wallace and Sullivan, 1985; Stiell and Berry, 1985; Diamond and Bradbury, 1992; Katovich and Morse, 1992; Mielke, 1993; Humble et al., 1994; de Groot and Zylstra, 1996]	<i>Pissodes strobi</i> The most serious economic insect pest of white pine. Larvae tunnel down the inner bark of the shoot, killing the leaders.
Sawfly [Houseweart and Knight, 1986]	<i>Diprion similis</i> . Foliage damage
Pine false webworm	<i>Acantholyda erythrocephala</i> Foliage damage
White pine sawfly	<i>Neodiprion pinetum</i> Foliage damage
Jack pine budworm	<i>Choristoneura pinus</i> (when growing near jack pine) Foliage damage
Eastern pine shoot borer	<i>Eucosma gloriosa</i> Growing shoot damage
European pine shoot moth	<i>Rhyacionia buoliana</i> Growing shoot damage
Pine leaf adelgid	<i>Pineus pinifoliae</i> (when growing near red or black spruce) Causes shoot damage
White pine aphids	<i>Cinaria strobi</i> Can cause mortality in young trees
Seedling debarking weevil [Houseweart and Knight, 1986; Pendrel, 1990]	<i>Hylobius congener</i> Can cause seedling mortality
Warren's collar weevil	<i>H. warreni</i> Damages roots
Pine root collar weevil	<i>H. radialis</i> Damages roots
Pales weevil	<i>H. pales</i> Damages roots
Mound ants	<i>Formica</i> sp. Damages roots
Zimmerman pine moth	<i>Dioryctria zimmermani</i> . Damages sapling stems
Fir coneworm	<i>D. abietivorelle</i> reduces seed production
White pine cone beetle	<i>Conophthorus coniperda</i> reduces seed production
White pine cone borer [Wilson, 1977; Martineau, 1984; Rose and Lindquist, 1984; Syme, 1985]	<i>Eucosma tocullionana</i> reduces seed production

Fungi	
Disease	Agent
White pine blister rust [Patton, 1961; Van Arsdel, 1961; Charlton, 1963; Gremmen and Kam, 1970; Anderson, 1973; Lehrer, 1982; Lavalée, 1974, 1986; Robbins, 1984; Gross, 1985b; Stiehl, 1985; Ostrofsky et al., 1988; Merrill, 1991; Katovich and Mielke, 1993; Myren et al., 1994; Liebhold et al., 1995; Berube, 1996; Bowling and Niznowske, 1996; Hummer, 1997; La and Yi, 1976; Yokota and Uozumi, 1976; Stephan and Hyun, 1983]	<i>Cronartium ribicola</i> . the most serious fungal disease of white pine. Has alternate host from the <i>Ribes</i> species as well as <i>Pedicularis</i> and <i>Castilleja</i> species.. Eradication of <i>Ribes</i> near white pine nurseries is a common control practice.
“Damping off” of emerging seedlings [Peterson, 1975]	<i>Fusarium</i> spp. <i>Pythium</i> spp <i>Rhizoctonia</i> spp. <i>Phytophthora</i> spp. <i>Cylindrocladium</i> spp.
Cytospora dieback	<i>Valsa</i> spp. disease of young seedlings
Tip blight	<i>Sphaeropsis sapinea</i> disease of young seedlings
Snow blight	<i>Phacidium infestans</i> disease of young seedlings
Rhizinia root rot	<i>Rhizinia undulata</i> disease of young seedlings
Needle casts	<i>Lopnodermium</i> spp. <i>Hypoderma</i> spp. <i>Cytospora</i> spp.
Brown spot needle blight	<i>Mycosphaerella dearnessii</i> Disease of foliage
Sooty mold	<i>Catenuloxylum semiovatum</i> Disease of foliage
Scleroderris canker	<i>Gremmeniella abietina</i> Disease of stems
White pine root decline [Hodges, 1986]	<i>Verticicladiella procera</i> Root disease
Armillaria root rot Belt fungus Tomentosus root rot Brown cubical root rot Black root stain [Syme, 1985; Hodges, 1986 and Myren et al., 1994]	<i>Armillaria mellea</i> complex <i>Fomitopsis pinicola</i> <i>Inonotus tomentosus</i> <i>Heterobasidium annosum</i> <i>Verticicladiella</i> spp.
Animals	
Common name	Agent
Moose	<i>Alces alces</i> use pine stands for cover
White-tailed deer	<i>Odocoileus virginianus</i>
Porcupine	<i>Erethizon dorsatum</i> may feed on bark
Snowshoe hares [Radvanyi, 1987; Bergerson and Tardiff, 1988]	<i>Lepus americanus</i> commonly feed on bark and buds of young trees
Eastern cottontail rabbit	<i>Sylvilagus floridanus</i> commonly feed on bark and buds of young trees
Red squirrel [Syme, 1985]	<i>tamiasciurus hudsonicus</i> damages shoots in removing cones
Seed-eating birds	Many bird species commonly eat large quantities of seed

E. Symbiotic Relationships - Mycorrhizae

Field data indicate that ectomycorrhizae formed by *Pisolithus tinctorius* increase survival and growth of *P. strobus* and other southern pine species better than natural ectomycorrhizae on routine reforestation sites in the southern U.S (Marx et al., 1977). In Canada *Laccaria* sp., *Hebeloma* sp., *Tuber* sp. and *Thelephora terrestris* form ectomycorrhizas with *P. strobus* seedlings grown in pot cultures, while *Phialophora finlandia*, an unidentified ascomycetous “red-type” fungus, and the E-strain form ectendomycorrhizas (Schelkle et al., 1996; Ursic and Peterson, 1997).

Some ectomycorrhizal fungi can suppress root-rotting pathogens of conifers. A study of natural mycorrhizal colonization and frequency of root rot on eastern white pine seedlings at a southern Canadian nursery revealed a negative correlation between *T. terrestris* and root rot. This suggested that the association of this ectomycorrhizal fungus with *P. strobus* roots might have some antipathogenic effects (Ursic et al., 1997). Additionally, removal of the basidiome of the ectomycorrhizal fungus *Laccaria bicolor* associated with container-grown eastern white pine seedlings induces a very rapid decrease in both net photosynthesis and stomatal conductance of the host plant (Lamhamedi et al., 1994).

Section VII – Domestication

Eastern white pine has been an attractive species for planting within its range, with up to 40 million seedlings shipped yearly for fibre production and Christmas trees (Eckert and Kuser, 1988). The species has also been used for shelter-belts and urban plantings, and has been used on a small scale in some European countries. Despite its very high timber value, management difficulties with control of white pine weevil and blister rust in planted stands have discouraged its use. Eastern white pine is thus a rather minor reforestation species, particularly in the northern parts of its range in Canada, where annual nursery shipments in Ontario, Quebec and the Maritimes are now well below 5 million. Nevertheless, the potential value of white pine planting and breeding is well recognised, and tree improvement programs for the species are maintained at some level throughout most of its range.

A. Deployment of reforestation materials

White pine has a long history as a species for reforestation, and nursery production techniques are well-established. In the early years, most planting stock were produced as bareroot seedlings (Coons, 1978), with 2+0 shipped from southern nurseries and 3+0 in the north, although 2+2 transplants have demonstrated superior performance in the field (Mullin and Howard, 1973, Mullin and Christl, 1982). Following developments in nursery technology, eastern white pine is now commonly produced from seed in containerised systems, in soil-less growing media. A variety of containers are used and stock is raised in both heated and unheated greenhouse structures. Cultural techniques have become highly sophisticated, ensuring that high-quality planting stock can be produced reliably and efficiently (Landis et al., 1989, 1990a, b, 1992).

Eastern white pine planting stock can also be produced by means of vegetative propagation. Much of the research in this area has been motivated by possible clonal deployment of individual genotypes with putative resistance to white pine weevil and blister rust. While older trees are often difficult to propagate using long-shoot cuttings, those from 2- to 3-year-old seedlings have long been known to root easily (Deuber, 1942; Patton and Riker, 1958b; Zsuffa, 1973; Kiang et al., 1974; Kiang and Garrett, 1975; Struve and Blazich, 1982). Propagation is also possible using fascicular shoots (Struve and Blazich, 1980, 1984). Growth and performance of rooted cuttings are comparable to planting stock raised from seed (Struve et al., 1984; Struve and McKeand, 1990).

Clonal propagation of eastern white pine can also be achieved through micropropagation of juvenile explant cultures derived from cotyledons, epicotyls and hypocotyls (Kaul, 1987, 1990; Webb et al., 1988). Techniques for the initiation of somatic embryos are also available, although whole plants have not yet been successfully recovered from these cultures (Becwar et al., 1988; Finer et al., 1989).

Some successful trials have demonstrated the potential of direct seeding as a regeneration technique for eastern white pine (Graber and Thompson, 1969; Horton and Wang, 1969; Graber, 1988), but stocking is often irregular (Torbet et al., 1995). Operational use has generally been regarded as a

failure and is not recommended (Waldron, 1974). Feeding losses to small mammals can be over 80%, unless the seeds are covered with soil at time of sowing (Graber, 1969).

B. Provenance transfer

Local seed sources are often not the preferred provenance for planting, and northerly transfers are often beneficial, except in the extreme. Sources from the southern Appalachians perform well in all but the most northerly locations, with high volume production and reduced branchiness (Sluder, 1963; Funk, 1971, 1979; Sluder and Dorman, 1971; Funk et al., 1975; Wendel and Cech, 1976; Wright et al., 1976, 1979; Kriebel, 1978; Williams and Funk, 1978; Funk and Jokela, 1979). However, faster-growing southern sources are not sufficiently hardy to thrive in the harsher continental climates above 41°N (Fowler and Heimbürger, 1969b; King and Nienstaedt, 1969; Jeffers, 1977). The use of seed zone controls to limit the transfers within regions of adaptation have been recommended for the northern part of the species range in Québec (Li et al., 1997).

Tests in Australia indicated that the best provenances are from the southern part of the natural range, although none are as productive as *Pinus radiata* (Matheson, 1977; Wright et al., 1979). In the Lower Saxony region of Germany, Appalachian Mountain sources below 39°N perform consistently well, while those from north of 45° perform poorly (Stephan, 1974; Genys et al., 1978).

In most of Europe, North American pines are considered to be fast growing tree species. In Romania, *Pinus strobus* is the second most productive species after Douglas fir, and has the least variation in annual radial increment and the lowest wood specific gravity of any commercial species. It is recommended on rotations of 40-60 years for pulpwood and 60-80 years for saw timber (Radu and Radu, 1972). In contrast, despite the extensive introduction and promising performance of *P. strobus* in Bohemia and Moravia, its wood has been grossly underrated by the woodworking industry, largely as a result of premature felling (Vytiskova, 1970). Of the 20 exotic Pines (9 from North America) growing in the central chernozem region of south central Russia, *P. strobus* has the fastest growth rate. However, exotic pines grown in Russia are significantly inferior in growth rate and yield to the local *P. sylvestris* (Lutkin et al., 1974). In the Lower Saxony region of the former German Federal Republic, *P. strobus* is not recommended for pure stands, partly because of the poor price paid for its timber and the unsaleability of thinnings; however, because of its fast growth, pleasing appearance, windfirmness, hardiness and general adaptability, it is strongly recommended for mixtures and particularly for the rehabilitation of recreation forests (Schumacher, 1974). As well, in provenance tests established in 1960 in Lower Saxony, growth of the best provenances of *P. strobus* was comparable or superior to that of local *P. sylvestris*, contrary to the situation in Russia (Stephan, 1981). Additionally, at two sites in Lower Saxony, differences between a rangewide sample of North American provenances were observed in height growth and mortality and attack by *Chronartium ribicola* (Stephan, 1974). *P. strobus* is recommended for wet or periodically waterlogged sites in the lowlands and hills of medium to low fertility in the former German Democratic Republic, especially those of extreme frost hazard (Thomasius and Hartig, 1979).

Section VIII – Summary

Eastern white pine is one of the most important tree species in eastern North America. It has the largest range of any North American species in subsection *Strobus*, the "white pines", and is the only representative on the eastern side of the continent. It is an outcrossing, wind-pollinated species that can transfer genes rapidly to neighbouring populations and to other related species. Eastern white pine is regarded as intermediate in its tolerance to shade, and natural regeneration is favoured by silvicultural systems that encourage partial shade during establishment and initial development.

Eastern white pine exhibits clinal variation patterns, generally correlated with latitude, although local seed sources are often not the best performers. Heritability estimates are moderately high at young ages and, while typically decreasing at older ages, are sufficient to predict considerable gains from recurrent selection. Significant genotype-environment interactions have been reported, but family ranks are generally stable across environments.

Best production is on medium-textured, well-drained soils, in cool, humid areas. White pine can occur as pure stands, or in mixture with several other conifer and hardwood associates, depending on site conditions and history of disturbance. It is a long-lived, successional species, but can be an aggressive pioneer on old fields. The white pine weevil and white pine blister are serious pests and are the major challenge for management of both natural and planted populations.

Eastern white pine is well-suited to artificial regeneration and it has a long history as a planted species throughout its natural range, both in forestry and urban applications. Tree breeding efforts have been targeted primarily at selection and interspecific hybridisation, in an attempt to produce varieties with resistance to the weevil and blister rust. Management difficulties have limited planting of eastern white pine, particularly in the north of its range, although seed orchards are maintained in all regions. Meanwhile, a long history of economic exploitation has resulted in fragmentation and reduction of population sizes in some areas, making genetic conservation of this species a growing concern.

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